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Manifestations of domination: Assessments of social dominance in rodents

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Abstract

Social hierarchies are ubiquitous features of virtually all animal groups. The varying social ranks of members within these groups have profound effects on both physical and emotional health, with lower-ranked individuals typically being the most adversely affected by their respective ranks. Thus, reliable measures of social dominance in preclinical rodent models are necessary to better understand the effects of an individual's social rank on other behaviors and physiological processes. In this review, we outline the primary methodologies used to assess social dominance in various rodent species: those that are based on analyses of agonistic behaviors, and those that are based on resource competition. In synthesizing this review, we conclude that assays based on resource competition may be better suited to characterize social dominance in a wider variety of rodent species and strains, and in both males and females. Lastly, albeit expectedly, we demonstrate that similarly to many other areas of preclinical research, studies incorporating female subjects are lacking in comparison to those using males. These findings emphasize the need for an increased number of studies assessing social dominance in females to form a more comprehensive understanding of this behavioral phenomenon.

Keywords

agonistic behavior; hierarchy; resource competition; social rank

1 | INTRODUCTION

The investigation of social hierarchies dates back to Thorlief Schjelderup-Ebbe's work in the 1920s characterizing social hierarchies in populations of chickens. Throughout this work, Schjelderup-Ebbe observed a strict, linear relationship of inter-group aggression, suggesting that each bird maintained a different social rank as a function of their rank within this aggressive order (the finding responsible for the colloquialism "pecking order" when referring to any social hierarchy).[1] It has since been well demonstrated that these hierarchies are an integral part of virtually all group-living animal species, and that a

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subject's rank within a given hierarchy may be characterized by quantifying their access to various resources and/or exhibition of aggressive behaviors, with higher-ranking, dominant animals acquiring larger proportions of said resources[2,3] and/or exhibiting higher levels of aggression toward their lower-ranking counterparts[4] and even colony intruders.[5]

Conceptually, the analyses of hierarchical relationships between rodents can be divided into two main categories: (1) Analysis of agonistic interactions and (2) analysis of differences in access to various types of resources, including territory, mates, standard chow, palatable food, and/or water. Agonistic behaviors can be directly measured in rodents, and highly aggressive rodents do have a tendency for increased access to resources.[5–8] However, the unequal distribution of resources in humans is not exclusively regulated by aggression of higher-ranking individuals.[9,10] Similarly, increased access to resources in rodents does not always necessitate overt aggression on the part of the high-ranking subject, suggesting that the assessment of aggression alone is not sufficient to identify a rodent's social rank. It should be noted, though, that the measures obtained during the assessment of differences in access to resources are often indirect. For example, higher scent marking or increased ultrasonic vocalizations in dominant animals (see Sections 4 and 8i) could reflect increased access to territory and mates, but these measures are not necessarily directly proportional to such access. In addition, the behaviors assessed in these resource competition tasks could reflect a state of the animal, rather than a trait: for example, competition for food may not exclusively reflect social rank, as performance in this assay can also be affected by an individual's sensitivity to food deprivation and/or their innate motivation to consume a given resource.

In the sections below, we describe the most frequently used tests of social hierarchy and dominance in rodents, as well as the relationships between them in various rodent species/strains and across both sexes (for a summary of this information, refer to Figure 1). Following the description of these assays, we synthesize this information to provide strategies for future studies and highlight opportunities to develop an improved understanding of social rank among both male and female rodents.

2 | AGONISTIC BEHAVIORS

One of the most commonly used methods to assess social rank among rodents is the analysis of agonistic behaviors (for schematic of common agonistic behaviors, see Figure 2(A)). Agonistic encounters consist of both offensive and defensive behaviors exchanged between two animals.[11,12] Offensive behaviors typically include lateral attacks, chasing, biting and barbering, whereas defensive behaviors typically include flight, freezing, and exhibition of submissive (lying on back) or defensive (upright with paws raised) postures.[12–16] Social rank is often determined following the observation of these behaviors during social interactions. However, experimenters have also used weight loss, the extent of barbering, and the number, severity, and location of scars/wounds following social interactions as indirect measures of dominance. Specifically, an animal is considered subordinate if it exhibits greater weight loss and/or has a higher number of severe wounds, while an animal is considered dominant if it experiences less weight loss and has a lower number of less severe wounds. Additionally, in rats, the wounds of subordinates are often located primarily on the tail, back, and flank, in comparison to dominants, for which wounds are primarily located on the head and snout.[17–34] For barbering, also termed fur trimming, whisker trimming, the Dalila effect, or over-grooming, a mouse is considered dominant if all fur and whiskers remain intact, and subordinate if fur loss and/or whisker shortening/loss are observed.[35–40] Notably, barbering is one of the only agonistic behaviors readily observed in female C57BL/6J mice.[35,36,38,41] On the other hand, barbering has also been shown to be unrelated to social dominance, rather, attributed to factors ranging from an unenriched environment to a manifestation of an obsessive–compulsive-like disorder or stereotypic behavior.[42,43] In fact, barbering is one agonistic behavior that is not thought to occur in a naturalistic setting, but is limited to laboratory mice.[43,44]

To assess social dominance relations between singly housed animals, a pair of subjects, typically same-sex, is placed in a neutral cage or arena to allow for social interaction, during which agonistic behaviors are scored. This design is especially useful for more aggressive species or strains, in that the length of agonistic interactions can be controlled by the experimenter. This model has been used to characterize social rank in male mice,[45,46] male gerbils,[47] male and female rats,[13,14,48,49] male and female mandarin voles,[50] male root voles,[51] and male and female hamsters.[52–58] These studies have revealed that dominant-subordinate relationships are readily formed for all male mice, rats, hamsters, gerbils, and mandarin voles under these conditions, and that these relationships are typically stable over time. In contrast, female rats are rarely reported to form these relationships, due to less frequent and severe agonistic interactions.[13,14] On the other hand, female hamsters and mandarin voles are naturally more aggressive, which results in the observation of strict dominant-subordinate agonistic relationships during same-sex interactions.[50,54,55] It must be noted that while these studies identify potential dominant-subordinate relationships between pairs of subjects, it cannot be conclusively stated that these relationships are reflective of the social hierarchies that emerge in socially-housed animals.

Thus, agonistic behaviors have also been analyzed in rodents that are housed in the same cage, but separated by barriers or partitions to prevent constant, direct physical contact. When these partitions are removed by the experimenter, subjects are able to interact directly, allowing for the observation of agonistic behaviors.[32,59–68] This assay has been used to identify dominance hierarchies in male Long Evans rats,[32,66] male BALB/cJ mice,[59] male NMRI mice,[63] male CD1 mice,[64] male large vesper mice (*Calomys callosus*),[65] male and female hamsters,[60–62,68] and male gerbils.[67] As in single-housed designs, these experiments are particularly useful when investigating social rank in highly aggressive species and strains, that if housed in standard group-housing conditions, would present the risk of severe injury or death of subordinate subjects.

Several studies have also assessed agonistic behaviors and social rank in pair- or group-housed rodents allowing for continuous, direct social interaction. These designs allow for agonistic interactions to be analyzed under two potential conditions: (1) Among the group and colony members only, or (2) following the introduction of an intruder rodent. In the former example, animals exhibiting the highest number of offensive behaviors toward their own cagemates are considered dominant,[69] whereas in the resident-intruder model, animals exhibiting the highest number of offensive behaviors toward the intruder are considered dominant.[21,70]

Analysis of spontaneous agonistic interactions and evaluation of wounds or barbering among cagemates has been conducted in group-housed male mice,[16,27,28,30,33,38,39,46,69,71–90] female mice,[16,38,39,86,91,92] male rats,[4,14,22–24,31,32,34,93–98] female rats,[14] male bank voles,[99] and female hamsters.[100,101] The majority of these studies observed strict linear dominance hierarchies in male mice, male rats, male voles, and female hamsters; whereas markedly less strict hierarchies—or no hierarchies at all—were observed among female mice and rats. In this context, linear refers to the structure in which there is an alpha (dominant over all cagemates), beta (dominant over all cagemates except alpha), and so forth, within the hierarchy.[86] In contrast, studies using the resident-intruder model have demonstrated that despotic, or exclusive, dominance hierarchies are formed in male rats and male and female mice,[21,91,102–104] where despotic refers to a single animal maintaining dominance over all other cagemates, with no differences in rank between these subordinates.[86]

Additional studies of social rank have been conducted using a mixed-sex design. These models are typically employed to potentiate agonistic interactions among male subjects and/or to provide more naturalistic housing conditions (refer to Figure 2(B) for a schematic of the visual burrow system, or VBS, a system often used in these types of experiments). As in same-sex studies, social rank can be determined by analyzing the spontaneous agonistic behaviors among the colony members[6,29,105–108] or the agonistic behaviors of colony members toward a stranger, "intruder" rodent in a resident-intruder test.[109,110] The vast majority of mixed-sex colony studies analyzing spontaneous agonistic encounters within a colony have revealed that strict, despotic social hierarchies are readily established among male rats and mice, while no hierarchies are observed among female rats and mice.[5–8,15,17,25,26,86,87,111–129] In contrast, female hamsters housed in mixed-sex pairs establish strong dominant-subordinate relationships, with females typically maintaining dominance over the male.[130] However, a resident-intruder study using mixed-sex colonies of Long Evans rats has demonstrated that one male and one female in each colony exhibit social dominance evidenced by increased aggression toward an intruder rat introduced to the colony.[109] Importantly, though, a female was only identifiable as dominant when all male colony members were removed from the cage during the resident-intruder test.[109] This finding demonstrates that the lack of observed social ranks among females in previous VBS studies is likely attributable to the testing conditions used: It seems that for this assay, all males must be removed from the environment during testing for a dominant female to emerge. These data suggest that social hierarchies can, in fact, form among female rats, but that the tests traditionally used to assess dominance in males may prove insufficient in detecting these dynamics in females.

Overall, these studies demonstrate that agonistic behaviors serve as a useful measure of social dominance in males of many rodent species, as well as in female hamsters and mandarin voles, and even female rats under certain testing conditions. As such, this method has proven generally less reliable in female mice, rats (when tested in the presence of males), and gerbils, suggesting that different measures should be utilized when assessing social rank in these populations. Lastly, it must be noted that severe injury or death of subordinate subjects is a considerable risk in studies using more aggressive strains and species. Therefore, in these subjects, single-housing, or modified group-housing settings where subjects are separated by partitions need to be used, in that they allow for constant supervision of agonistic encounters.

3 | TUBE TEST

The tube test was first developed by Lindzey and colleagues in 1961 to characterize social dominance in male and female mice,[131] and has since been employed to assess social rank in different mouse strains and other rodent species (see Figure 3(A) for tube test schematic).

For this assay, experimenters use a clear, plastic tube, typically 30 cm in length for smaller rodents. The appropriate diameter is determined so that there is only room for one subject to pass through the tube at a given time.[131,132] Before testing, rodents are first habituated to the apparatus and trained to cross through the tube individually. Subjects are often presented with a food reward during this training process to promote crossing through the full length of the tube.[131,133–135] Animals are then paired to undergo testing, during which each subject is placed on opposite ends of the tube and allowed to approach its conspecific toward the center of the tube. The subject that subsequently forces its competitor out of the tube is considered the winner (dominant), and the subject forced out of the tube the loser (subordinate). If examining social rank among a group of 3 or more subjects, multiple tube tests are conducted using a round-robin design to ensure that tests take place between all members of said group.[132]

The tube test has been used to evaluate social rank in male and female mice,[36,37,39–41,45,70,131,132,136–149] male and female prairie voles,[150] male and female rats,[133,134,151,152] male hamsters,[135] and male gerbils.[135] In these models, a point system is often used to express the social rank of a subject relative to other group members. For example, the winner of each test can be assigned 1 point, and the loser 0 points. Following the completion of all tests between group members, each subjects' points are added together to determine its social rank within the group. Therefore, in a group of four subjects, the most dominant animal would obtain 3 total points, and the most subordinate 0 points following tube tests with all other group members.[37,131,132] Alternatively, David's Score (DS) can be used to calculate social rank following tube tests. DS is a slightly more complex measure that calculates dominance score based on a subject's proportion of wins to losses following repeated social interactions (for detailed information on DS calculation, refer to Reference 153).

Importantly, social ranks determined using this measure have been shown to positively correlate with ranks determined from other dominance measures, such as the warm spot test, urine-marking, and ultrasonic vocalization measures.[37,132,138,142,143] The relationship between tube test ranks and food/water competition ranks remains less clear, however, and tends to vary between species and the type of reward used. For example, a negative correlation between tube test and food competition ranks has been reported in male DBA and albino mice when the food reward is standard rodent chow.[45] In contrast, in studies using male Lister rats[151] or male ICR mice,[145] ranks obtained following palatable food/liquid competition were positively correlated with tube test ranks.[145,151] These inconsistencies are also observed in water competition tasks, in which no relationship between water competition rank and tube test rank is seen in male gerbils, though this relationship is positively correlated in male hamsters.[135]

Contradictory results have also been obtained for the relationship between tube test rank and ranks determined from displays of agonistic behaviors, with certain studies revealing a positive correlation,[37,40,142] and others finding a negative correlation or no relationship between these measures.[41,45] Of note, the studies that observed positive correlations between agonistic behavior rank and tube test rank were conducted using male C57BL/6 mice. In contrast, the studies that observed a negative correlation[45] or no relationship between these measures[41] were conducted using male DBA and albino mice[45] or male and female C57BL/6 mice,[41] respectively. Taken together, these findings suggest a potential role of sex and/or strain in the correlation between social ranks determined from the tube test and those determined from agonistic behavior measures.

Overall, the tube test serves as a useful model for assessing social dominance in males and females and across various rodent species, proving especially useful if the subject population is less prone to agonistic behaviors. Even among rodents that readily exhibit aggression, the tube test presents certain advantages, in that animals are not susceptible to injury as they would be if using assays such as agonistic behavioral assessment. It must be considered, though, that species, strain, and sex can determine the generalizability of tube test results to other dominance measures.

4 | SCENT-MARKING

Patterns in scent-marking, or urine- and flank-marking, in rodents have also been used as measures of social dominance (for schematic of scent-marking assay, refer to Figure 3(B)). Urine-marking is most often used to characterize the social rank of male mice,[28,37,84,85,138,142,154–156] but it has also been used to assess dominance in in female mice,[157] male bank voles,[99,158,159] and male root voles.[51]

In this assay, two subjects are placed in a neutral, clean cage separated into two compartments. The rodents remain in their respective compartments for a test period allowing for urine collection, ranging from 2 to 22 h.[28,37,84,85,142,158] However, urine-marking can also be assessed in a single subject, placed in a test cage alone for 3 min to 2 h.[51,154–157] This design also allows for the assessment of counter-marking, or scent-marking over an experimenter-presented urine sample from a conspecific, which can denote social rank as well.[155,157]

Regardless of the setup used for testing, cages are lined with filter paper so that urine markings can be subsequently analyzed by visualization with UV light. The number of urine marks reflects social rank, with a higher number of marks indicating dominance, and a lower number of marks indicating subordinance.[28,85,99,156] Counter-marking studies have also revealed that subjects identified as dominant based on agonistic behaviors will urine-mark over virtually any urine sample presented, regardless of the rank of the animal from which the sample was collected, while subordinate subjects will not.[155,157] Additional studies have shown that dominants, again the rank of which is determined based on displays of agonistic behavior, typically scent-mark throughout the entirety of the test arena, with concentrations close to the partition, while the urine marks of subordinates are often confined to the corners of the arena.[28,158,159] Interestingly, in the one study using females, urine-marking patterns of dominants were similar to those observed in dominant males, in that female dominants, identified based on agonistic behavior analysis, exhibited a higher number of urine-marks than subordinates, while also exhibiting counter-marking behaviors.[155,157] Each of the studies mentioned above has demonstrated that social rank determined by urine-marking positively correlates with that determined by agonistic behavior analysis or the tube test, with the exception of the study using male root voles. In this experiment, no relationship was observed between social rank determined by agonistic behavior analysis and social rank determined by urine-marking,[51] a finding suggesting that urine-marking assays may not be a reliable measure of social dominance in all species. Notably, of the one study conducted using female mice, urine-marking was compared between breeding and nonbreeding females,[157] demonstrating that additional urine-marking studies in females of the same breeding status should be conducted to further investigate the effect of social rank on this behavior in females.

In contrast to urine-marking, flank-marking has been used to characterize social rank in male hamsters,[53,60,62,160–162] female hamsters,[52,61] and male gerbils.[121] Flank-marking involves the rubbing of an animal’s dorsolateral flank glands on objects and/or areas within their environment.[161] As such, this behavior is typically scored as the total number of flank-marks exhibited by each subject during social interaction,[61,62] when placed in an open field,[121] or when placed in the empty, dirty homecage of a conspecific.[52,161] It has been consistently demonstrated that male and female hamsters and male gerbils that exhibit the most flank-marks are also dominant in agonistic encounters. Notably, while female gerbils also possess flank glands, they appear to use scent-marking behavior not to communicate dominance, but rather as a means to defend the nest during gestation and lactation,[163] a finding suggesting that while flank-marking is a useful measure for social dominance in male and female hamsters and male gerbils, this assay would not be useful in assessing dominance for female gerbils.

Collectively, these data suggest that while scent-marking assays can prove useful in characterizing social rank, their validity is dependent upon the sex and species—and potentially breeder status—of subjects used.

5 | STANDARD FOOD AND WATER ACCESS PRIORITY/COMPETITION

Resource competition assays, or food and water access priority/competition, are additional means of characterizing social dominance in rodents. These tasks almost always involve food or water deprivation, most often for 22–23 h periods,[135,164–168] or food restriction, during which subjects are maintained at approximately 80%–85% free-feeding body weight.[91,169,170] Animals are then given access to standard rodent chow or water for a short period of time, typically 5 min,[45,164–166,171,172] to induce resource competition in a water- or food-deprived state. In fact, only one study of food/water competition has been conducted in non-deprived conditions.[100] Overall, these assays have been conducted in the homecage of group-housed subjects,[96,135,173,174] or in a neutral test cage, allowing for testing between novel conspecifics[45,165–169,171,172,175–177] or cagemates[169,176] (see Figure 3(C) for schematic of standard chow/water competition assay).

The way in which food or water is presented in most tests allows for only one subject to access the resource at a given time, and the dominant can be identified as the subject that maintains control of the resource. While one of the first publications on food competition described using subjects' changes in body weight after testing as an indirect measure of amount of food consumed, and thus social dominance,[178] no subsequent studies have relied on this measure. Specifically, social dominance has since been determined by measuring the total amount of food or water consumed or taken,[100] the number of instances in which a subject successfully gains access to the resource,[109,171,174,177] the number of offensive (dominant) or defensive (subordinate) behaviors exhibited during competition,[179] the time spent consuming or maintaining control of the resource,[45,96,109,164–166,168,172,173,175] or the order of access, with dominants accessing food/water first.[109,135]

An additional study has employed an operant self-administration model, in which rats were trained to lever press for the delivery of a food pellet. For testing, pairs were then placed in the self-administration chamber and allowed to compete for the delivery of food pellets, and the subject consuming the greatest number of reinforcers was considered dominant.[170] Lastly, modified tube test procedures have been used to assess food competition for standard pellets of chow.[91] However, in this assay, dominance was determined based on the number of aggressive behaviors exhibited while competing for the food pellets.[91]

Food and water access priority tasks have been used to assess social dominance in male rats,[96,109,164–167,170,172,173,175,176,179] female rats,[109,166,167] male mice,[45,174] female mice,[91] male hamsters,[135,169] female hamsters,[100] and male gerbils.[135] The results of this assay tend to vary across studies, however, suggesting that factors such as species, strain, housing conditions, experimental setup, and cohort variability may affect the outcome of resource competition. For example, one study using singly-housed Wistar rats documented the emergence of stable dominant-subordinate relationships,[166] while another using singly-housed albino rats did not.[167] Additionally, in a study by Candland and Bloomquist, no stable hierarchies were observed among large groups of rats or hamsters ($n = 10$),[169] suggesting that group size may also impact the results of food competition tasks. Further, a subsequent study demonstrated that resource competition tasks can serve as effective measures of social rank in larger group sizes, and that larger groups merely require a greater number of tests to reach stability.[172]

Similarly, the generalizability of these assays' results to other measures of social dominance varies across species. Specifically, social ranks obtained from food/water access priority have been shown to positively correlate with social ranks based on agonistic interactions in male mice,[45] but not in male rats[96,109] or female rats.[109] Additionally, positive correlations between tube test social ranks and water competition social ranks have been observed in hamsters, but not gerbils.[135] Perhaps these differing outcomes also reflect potential effects of sex, species, and/or strain on an animal's sensitivity to food/water deprivation or food restriction. For example, these manipulations have been demonstrated to serve as stressors,[180–183] inducing anxiety-like behavior[184] and increases in plasma corticosterone levels,[185] which in turn could differentially affect animals' motivation to compete for food and water. Overall, these food/water competition tasks seem to vary substantially between species, strain, and overall experimental design, suggesting that they may not serve as the most reliable measure of social dominance in rodents.

6 | FORAGING

Patterns in food/water consumption under ad libitum conditions in group-housed animals may serve as a more reliable measure of social dominance. For example, it has been repeatedly shown that dominant male rats (based on exhibition of agonistic behaviors) consume significantly more food/water and have more frequent bouts of consumption than their subordinate cagemates.[5–8] Based on these previous findings, a study by Lee and colleagues[90] analyzed patterns of food and water intake in male mice of differing social ranks. They found that mice considered dominant based on exhibition of agonistic behaviors had a significantly higher number of eating and drinking bouts than subordinates.[90] Additionally, periods of quiescence, or inactivity, were significantly shorter in dominant mice compared to subordinates.[90] Overall, these data suggest that additional studies testing food and water intake under ad libitum conditions should be performed in females, as well as other rodent species and strains, to determine whether these measures are indicative of social rank in additional subject populations.

7 | PALATABLE FOOD AND LIQUID COMPETITION

Palatable food and liquid competition assays have also been used to assess social dominance in male mice,[186–188] rats,[109,151,173,179,189–203] and Brandt's voles,[204] with fairly consistent results across strains and species, in that dominant-subordinate relationships are consistently observed following testing (schematic of palatable food/liquid competition illustrated in Figure 3(D)). Only one study has been conducted using females, in which female Long Evans rats were co-housed with male Long Evans rats for the entirety of the study, *except* during palatable food competition.[109] This assay has yet to be conducted in singly-housed or same-sex group-housed females.

Palatable food competition can be conducted within the homecage, and assess dominance relationships between cagemates,[109,173,190,193–199] as well as in neutral environments to assess dominance among novel conspecifics[179,191,200–202] or cagemates.[151,186,187,189,192,203,204] Generally, foods and liquids with high levels of sucrose, such as chocolate, sweetened condensed milk, or graham crackers, are used as the object of competition, as rodents have an innately high preference for sucrose.[205,206] However, palatable foods with lower sucrose content, such as cheese, have also been used successfully in these assays.[187] Regardless of the tastant presented, all competition assays require an initial habituation period in which subjects are exposed to the palatable food or liquid prior to competition tasks to avoid neophobia during testing and to ensure that all animals exhibit a similar preference for the food under noncompetitive conditions. As a caveat, it should be noted that motivation to consume a given reinforcer (e.g., through the use of a progressive ratio schedule of operant reinforcement) has not been examined, and thus should be considered as a potential factor contributing to each subject's performance.

For testing under non-deprived conditions, subjects are either transferred to a neutral test cage, or the standard chow and water bottles of the homecage are removed, so that only the palatable food/liquid is available for consumption. During these food competition tests, the amount of food presented, how it is presented, and how social dominance is scored, vary across studies. For example, one set of studies involve the presentation of one sucrose pellet every 2 min for a 1 h test session, resulting in the delivery of 30 total pellets per session to each group.[195–199] Thus, the rat consuming the highest number of sucrose pellets during a 1 h session is considered to be the dominant subject.[195–199] A pair of rodents can also be tested under modified tube test conditions, with each subject approaching a 0.4 g piece of cheese placed in the center of a plastic tube, and the mouse consuming the cheese being identified as dominant.[187] Lastly, food competition tasks can involve the presentation of a predetermined amount of food (for example, 3 g graham cracker crumbs[201] or eight pieces of chocolate cereal[179]) in a central location within a neutral cage or the subjects' homecage. Importantly, the food is presented so that only a single subject can access or consume the reward at a given time. The food is typically made available for 10–15 min,[179,201,204] or until all the food has been consumed. With this design, the dominant can be identified using several measures: time spent eating food,[201] time spent maintaining possession of food,[109,186,188] amount of food consumed,[179] and order of access, with dominants accessing food first.[109,190,204]

Similarly, palatable liquid competition tests also vary in regard to the amount of solution presented, how it is presented, and how dominance is scored. For example, in a study by Askew and colleagues, pairs of rats were trained to compete for sweetened condensed milk solution in an operant self-administration model, such that the animal with the highest number of active lever presses, reinforcers earned, and solution consumed was identified as dominant.[191] Additionally, a pair of rodents can be tested under modified tube test conditions, with each subject approaching a feeder containing sweetened milk in the center of a plastic tube.[192,200,202] As with palatable food competition tests, the sippers are designed so that only a single subject can access and consume the reward at a given time. Thus, the animal that spends the higher amount of time at the feeder during the test period is considered dominant.[192,200,202] Lastly, a standard bottle/sipper containing palatable liquid can be presented in the homecage or a neutral test cage, with social rank being determined based on the volume of solution consumed or the amount of time spent consuming solution[151,189,193,194].

It must be noted, though, that several studies incorporate food or water deprivation prior to competition tasks, with periods of deprivation ranging from 8 to 23 h,[109,173,186,187,192,203,204] while an additional study chose to employ food restriction, maintaining subjects at 95% body weight throughout the entire experiment.[191] Both food/water deprivation and food restriction strategies are thought to increase the motivation to consume the food/liquid presented during testing, though many palatable food/liquid competition studies do not incorporate food or water deprivation given rodents' innate, high motivation to consume most substances used in these tasks.

Overall, palatable food and liquid competition tasks have proven reliable in assessing social dominance in various rodent species, with either dominant-subordinate relationships or linear hierarchies being observed in nearly all groups examined for each study. Nevertheless, in one study that compared social rank based on agonistic behaviors to social rank based on palatable food competition, results were not consistent.[109] Notably, this study tested mixed-sex groups of male and female rats that were only housed with same-sex animals during the palatable food competition test,[109] suggesting that factors such as housing condition and breeding/maternal status, may influence an individual's performance in this assay. Lastly, as with many other assays outlined in this review, more studies that incorporate female subjects are warranted to determine whether this assay is a suitable measure of dominance for this sex.

8 | ADDITIONAL MEASURES

8.1 | Ultrasonic vocalizations

Two studies have measured 70 kHz ultrasonic vocalizations (USVs), often termed "courtship songs," of male mice to determine social dominance, as this USV frequency is used by male mice during mating behaviors.[207,208] More specifically, when presented with a female, dominant male mice (rank determined based on display of agonistic behaviors) emit significantly more and longer-lasting 70 kHz USVs, and have shorter latencies to emit the first USV when compared to subordinate males,[37,208] demonstrating the potential of 70 kHz USVs to serve as a measure of social dominance in male mice (refer to Figure 3(E) for schematic of this USV assay).

While rats are also known to emit USVs of various frequencies, the purpose of these USVs is completely different from that in mice.[207] For example, subordinate rats have been shown to exhibit 22 kHz frequency USVs during agonistic interactions in which they are being defeated by a dominant, as well as in response to other aversive stimuli.[207] Additionally, while these 22 kHz frequency USVs may serve as a potential measure of social rank, it can be challenging to identify the precise location of a given USV's source,[209] suggesting that USVs may not be the most reliable measure of social rank in rats since such data are required to be collected while subjects are in close proximity and undergoing agonistic interactions.

8.2 | Warm spot test

A more recent study by Zhou and colleagues has developed an additional method of assessing social dominance: the warm spot test.[143] This assay involves two test cages, the floors of which are cooled to 0°C. A group of four male mice is placed in one of the cooled cages for 30 min before being transferred to an additional cooled test cage. In this additional cage, a nestlet 5 cm in diameter is placed in a corner that has been heated to 34°C. Mice remain in this test cage for 20 min while their behavior is recorded. As animals have an innate drive to stay warm,[210,211] this assay can be considered a type of resource competition.

Thus, dominance is scored based on the amount of time each animal spends in the warm spot of the cage, such that the most dominant animal spends the most time in this area, while the most subordinate animal spends the least amount of time in this area[143] (see Figure 3(F) for schematic of warm spot test). This method warrants future studies examining its reliability in females as well as in other rodent species and strains.

8.3 | Shock avoidance

Social rank has also been examined in singly-housed male C57BL/6 mice using a shock avoidance model.[212] Briefly, a pair of subjects is placed in a neutral apparatus equipped with a grid floor that administers a footshock and an escape platform on which an animal can jump to avoid shock. Because the platform is designed to accommodate only one mouse, a subject is considered to be dominant if it maintains control of the escape platform throughout the test session[212] (see Figure 3(G) for schematic of shock avoidance assay). To our knowledge, this assay has only been used as a measure of social dominance once, with male C57BL/6 mice, so the generalizability of this assay to females as well as to other species and strains of rodents remains unknown.

8.4 | Nesting

It has also been demonstrated that dominant female mice (bred on a mixed 129 × Black Swiss background) express different nesting behaviors than their subordinate counterparts. Specifically, subjects identified as dominant based on frequency of offensive agonistic behaviors consistently constructed all nests while also “corralling” subordinate cagemates to these nest areas.[91] This finding suggests that nesting behaviors may serve as a potential measure for social dominance, at least in certain strains of female mice. Though as with the shock avoidance assay outlined above, the applicability of this assay for males and different rodent species or strains remains unknown. Additionally, it must be noted that nesting behavior has been used extensively in other areas of research to assess general well-being,[213] and even in models of autism spectrum and obsessive–compulsive disorders.[214]These data suggest that much more work is needed to determine whether this behavior is a manifestation of an animal’s social rank, an animal model of stereotypies associated with certain human neurological disorders, or a different phenomenon altogether.

9 | CONCLUSIONS

The assays outlined above can be thought of to belong to two broad categories used in measuring social dominance: (1) those based on agonistic interactions, or “aggressive” dominance and (2) those based on resource competition, or “competitive” dominance.[215] While it may seem initially surprising that the ranks obtained from these two types of measures do not always positively correlate, the authors refer to an observation made by J. P. Scott in his 1966 review on agonistic behavior in rodents: The agonistic behavior measure is assessing *animal-directed* behavior,[216] and can be interpreted as the subject’s attempt to decrease subsequent competition for resources.[217] In contrast, the resource competition measure is assessing *object-directed* behavior, in that in that a conspecific represents a direct obstacle to a particular resource of interest.[216] Therefore, it can be argued that resource competition assays do not disregard agonistic behavior, rather, that they incorporate the assessment of additional behaviors involved in the drive to obtain resources.[216] Additionally, the propensity to display overt agonistic behaviors varies as a product of sex, species, and strain, suggesting that resource competition assays may serve as a more widely applicable measure of social dominance due to their capacity to be employed in a variety of subject populations.

One of the primary findings of this review was that while a vast amount of the literature has been conducted in the area of social dominance in rodents, the use of female subjects —with the exception of hamsters—remains grossly underrepresented. While this deficit is in part attributable to the less aggressive nature of most female rodents in comparison to males,[218] it is also likely due to the historical disregard of sex as a biological variable in virtually all fields of research.[219,220] Therefore, increased studies using resource competition assays, which do not require the display of aggressive behavior, are greatly needed to better characterize to social dominance in females.

We also feel it is important to interpret the findings from these experiments within the larger context of the naturalistic ecology of the rodent species being studied. To quote a review on ecological validity regarding social interaction tests in rodents, “even though not all experiments have to be ecologically valid, ecological perspective is crucial for the design and interpretation of research programs.”[221] In designing and conducting this type of experiment, researchers must appreciate the role of each rodent species’ ecology in their social behaviors, as well as how these species’ behaviors are potentially altered by years of inbreeding, the laboratory setting, and different housing conditions.[221,222]

Lastly, the authors would like to emphasize the importance of conservative interpretation of data obtained from these assays, particularly if attempting to make translational applications. We suggest that the measures outlined here are most useful when applied in reference to the specific rodent species used for a given study, rather than as a model for a human condition. Assessments of social dominance best serve to inform researchers about that specific species’ behavior and how an individual’s social rank may affect other variables with high translational value (i.e., stress responsivity or depressive-like behavior). Considering all of these factors in both experimental design and data interpretation will contribute greatly to progress in understanding social hierarchies among various rodent species.

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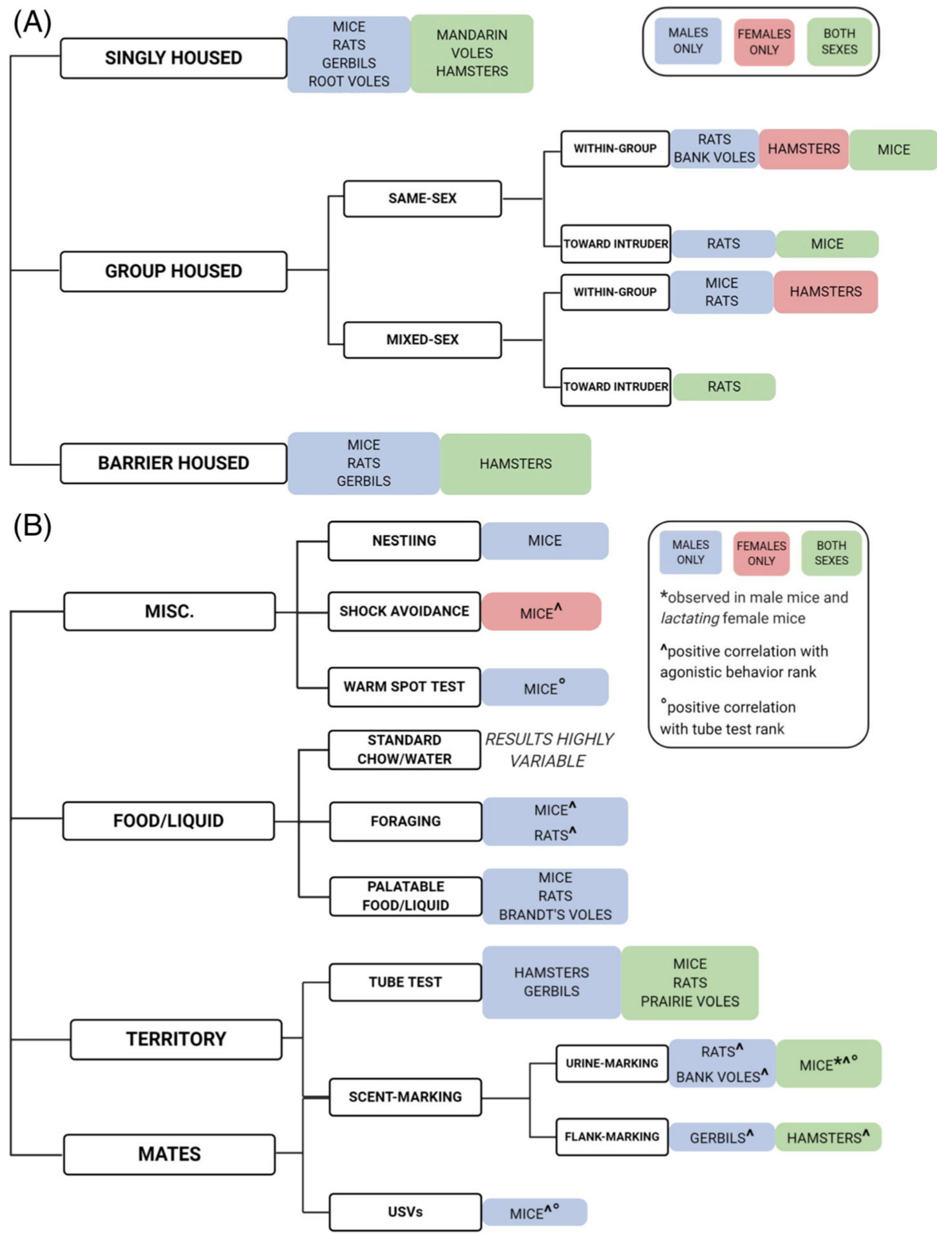

FIGURE 1.

Summary of species and sexes used in each measure of social dominance.

(A) Agonistic behavior.

(B) Resource competition

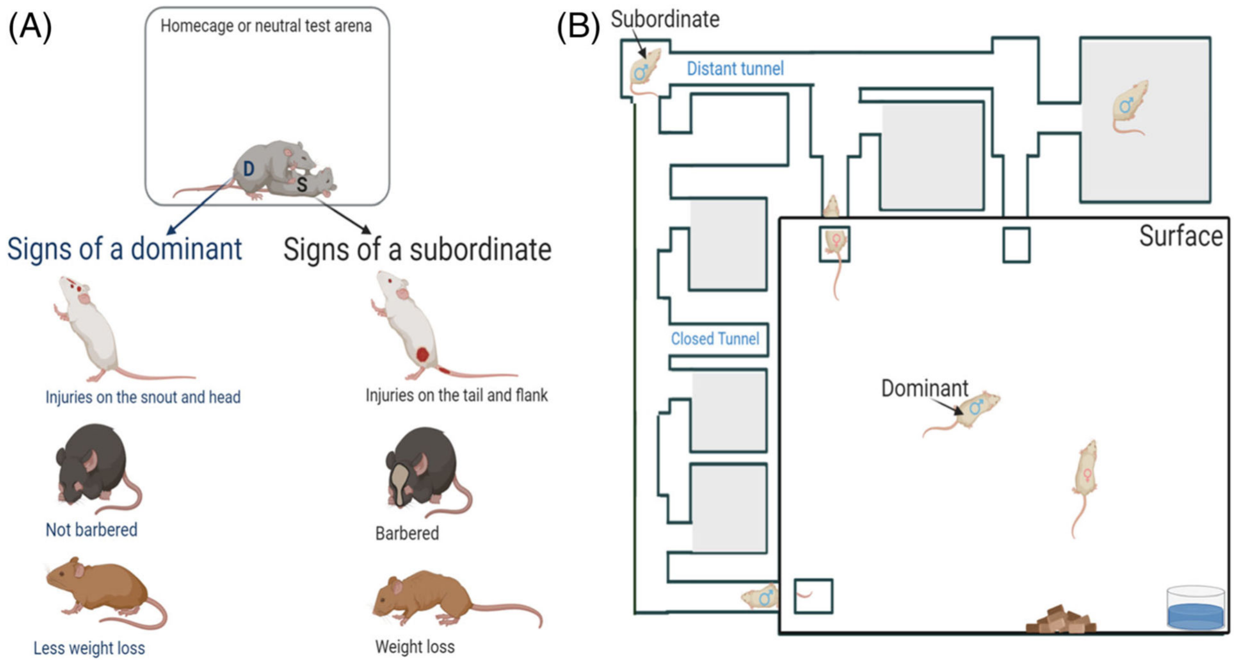

FIGURE 2.

Schematics of experimental setup for agonistic behavioral analyses. (A) Common examples of agonistic behaviors exhibited by dominant and subordinate subjects. Often conducted in a standard homecage or neutral arena. (B) Example of visible burrow system (VBS), a group-housed, mixed-sex design that promotes strict, despotic hierarchies among male subjects. In addition to the agonistic behaviors outlined in part (A), dominant and subordinate subjects in the VBS also spend differing amounts of time on the surface/in the tunnel system

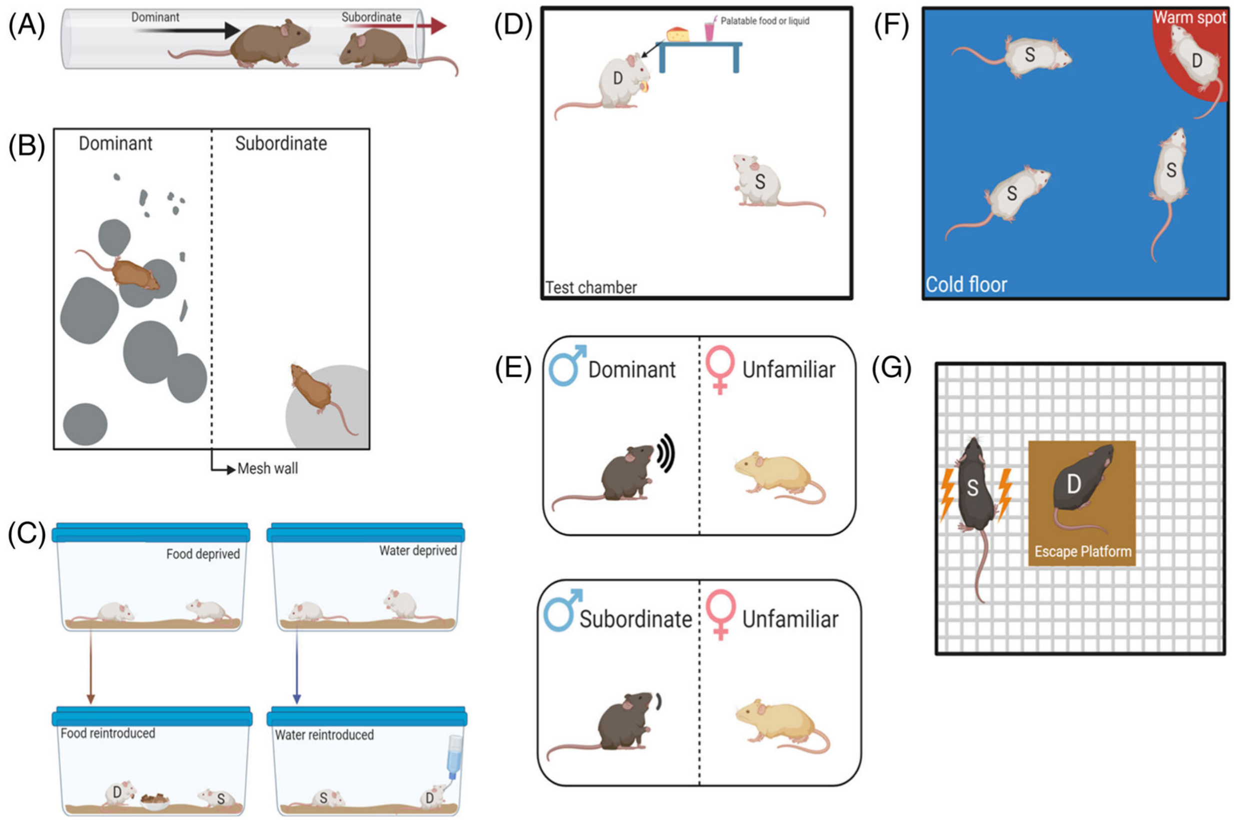

FIGURE 3.
Schematics of experiment setup for resource competition assays. (A) Tube test. (B) Scent-marking. (C) Standard chow/water competition. (D) Palatable food competition. (E) 70-mHz ultrasonic vocalizations. (F) Warm spot test. (G) Shock avoidance